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Asymmetry in Male Fiddler Crabs is Related to the Basic Pattern of Claw-waving Display

SATOSHI TAKEDA[1] AND MINORU MURAI[2]

[1]*Marine Biological Station, Tohoku University, Asamushi, Aomori 039-34, Japan and* [2]*Department of Biology, Faculty of Science, Kyushu University, Hakozaki, Fukuoka 812, Japan*

Abstract. Morphological asymmetry was correlated with the pattern of claw-waving display in males from five species of fiddler crabs: three vertical wavers (*Uca urvillei, U. dussumieri, U. vocans*), a lateral waver (*U. annulipes*), and an intermediate waver (*U. tetragonon*). On the first, second and third ambulatory legs of male lateral waver crabs, the distance between the inner edge of the basis and the outer edge of the merus was larger on the side bearing the major cheliped than it was on the side with the minor cheliped. A similar asymmetry was observed in male intermediate waver crabs, but only the first ambulatory leg was involved. This morphological asymmetry is clearly related to the style of waving adopted by these crabs. When lateral wavers display, the weight of the major cheliped (which forms about one-third of the total body weight) is carried largely by the anterior ambulatory legs on the same side of the body, but the imbalance of weight during display is less in the intermediate waver. In the vertical waver crab horizontal motion of the major cheliped occurs relatively rarely; thus there is hardly any additional load on the ambulatory legs, which showed no asymmetry.

However, the total length of the five sterna bearing thoracic legs tended to be larger on vertical waver males than on the female crabs. Thus the sterna of male crabs bulge outwards more than those of female crabs, and the angle between the sternum bearing the cheliped and the ground surface is larger in male crabs than in females. This may be an adaption enabling the cheliped of the male to be raised higher during the waving display.

Introduction

A characteristic feature of the genus *Uca* (Ocypodidae; Brachyura) is hypertrophy of one of the male chelipeds, resulting in a striking asymmetry (Crane, 1975). The hypertrophic, or major, cheliped plays a very important role in antagonistic and courtship behaviors (Crane, 1957, 1975), especially as a distinctive indicator of the male sex during the breeding season (Salmon and Stout, 1962).

The mechanism determining which of the chelipeds becomes hypertrophic has been examined in some species (Morgan, 1923, 1924; Yamaguchi, 1977; Ahmed, 1978), and the development of the asymmetry has been analyzed by monitoring the growth rate of the major cheliped relative to that of the carapace (Huxley and Callow, 1933; Tazelaar, 1933; Miller, 1973). In addition, the first and second ambulatory legs are longer on the side bearing the major cheliped than they are on the contralateral side in male *U. pugilator* (Yerkes, 1901; Duncker, 1903; Huxley and Callow, 1933; Miller, 1973), and in *U. pugnax* (Yerkes, 1901; Tazelaar, 1933) in North America. This asymmetry of the ambulatory legs was thought to help in raising the major cheliped higher, thus displaying it to more crabs (Miller, 1973).

Crane (1957, 1975) divided *Uca* into two groups based on the male's claw-waving display; *i.e.*, into vertical and lateral waving species. *U. pugilator* and *U. pugnax*, with asymmetry of the ambulatory legs as well as the chelipeds, form the lateral waving group (Crane, 1957, 1975). On the other hand, the ambulatory legs of male crabs of the vertical waving group have not yet been examined for possible asymmetries.

In this study, the degree of asymmetry of certain morphological characters, including the length of the ambulatory legs, was determined and compared among five species of *Uca* with different patterns of claw-waving display. Three of the five species were vertical wavers, one species was a lateral waver, and one exhibited an intermediate type of waving display.

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Materials and Methods

Crabs of five species, *U. urvillei*, *U. dussumieri*, *U. vocans*, *U. tetragonon* and *U. annulipes*, were collected on the seashores in Thailand (Table I). Larger individuals were selected for examination, since the degree of asymmetry in male fiddler crabs increases with body growth (Miller, 1973). Crabs lacking thoracic legs or those with degenerate, atypical thoracic legs were excluded.

U. urvillei, *U. dussumieri* and *U. vocans* are vertical wavers, *U. annulipes* is a lateral waver, and *U. tetragonon* is an intermediate (Crane, 1957, 1975). The proportion of right-handed and left-handed male crabs was nearly equal in *U. urvillei*, *U. dussumieri* and *U. annulipes*, and almost all male *U. vocans* and *U. tetragonon* are right-handed (Takeda and Yamaguchi, 1973; Frith and Frith, 1977).

Two indices of body-size were measured: carapace width (Fig. 1A); and the whole body wet-weight. The wet weight of the cheliped cut off between ischium and basis was also measured. Several morphological measurements were made (Fig. 1). These measurements on the right and left side of each individual include: three dimensions on the minor cheliped or ambulatory leg (Fig. 1B); body depth (Fig. 1A); carapace depth (Fig. 1A); and the length of each sternum bearing thoracic legs (Fig. 1C).

These measured values were normalized with respect to the wet-weight or carapace width. To determine the degree of asymmetry, the ratio of the values on the major cheliped side to the values on the opposite side in male crabs, and the ratio of the values on the right side to those on the left side in female crabs, were calculated for each individual. These data were examined for significance with Student's *t*-test.

Results

The carapace width and body wet-weight of individuals differed among the five species of *Uca* (Table II).

The weight of the major cheliped relative to the whole body wet-weight increased in the following order: *U. tetragonon* ≦ *U. dussumieri* ≦ *U. urvillei* ≦ *U. annulipes* ≦ *U. vocans* (Table III). The relative weight did not differ widely among the species of vertical, intermediate, and lateral wavers. The relative weight of the minor cheliped did not differ significantly ($P > 0.05$) among individuals of the same sex in four species, but *U. tetragonon* had a larger minor cheliped than the other four species ($P < 0.05$).

The relative dimensions of the minor chelipeds were larger in female crabs than in male crabs in each species ($P < 0.05$). The smaller values in male crabs resulted from their larger whole body wet-weight, which included the weight of the major cheliped.

The chelipeds of male crabs had a remarkable asymmetry ($P < 0.001$), and the ratio of major cheliped weight to minor cheliped weight increased in the order of *U. tetragonon* < *U. annulipes* ≦ *U. dussumieri* ≦ *U. urvillei* ≦ *U. vocans*. The smaller ratio in male crabs of *U. tetragonon* ($P < 0.05$) was caused by their having heavier minor chelipeds than the other four species. However, the intensity of asymmetry did not differ among the species with the different display patterns. In female crabs of all five species, the asymmetry ratio was near 1.0, which indicates the chelipeds were the same size.

Considering the total length of the ambulatory legs, which was calculated by adding the lengths of the I, II and III-sections of each ambulatory leg (Fig. 1B), asymmetry was perceptible ($P < 0.05$) only in first (ratio $= 1.04 \pm 0.02$ (mean ± the 95% confidence interval)) and second ambulatory legs (ratio $= 1.02 \pm 0.01$) of male *U. annulipes* (Fig. 2), and the ambulatory legs of the side bearing the major cheliped were longer than those of the opposite side. Moreover, for each section of the ambulatory legs, asymmetry was present in the I-section of the first, second and third ambulatory legs of male *U.*

Table I

Materials, display form and handedness in Uca *spp.*

Species	Display	Handedness	Specimens	Location	Date
U. urvillei	vertical	random	6 males 7 females	Ao Nam Bor[1]	1990. Sep.
U. dussumieri	vertical	random	9 males 9 females	Smare Kaow[2]	1987. Oct.
U. vocans	vertical	right	8 males 6 females	Ao Nam Bor[1]	1990. Sep.
U. tetragonon	intermediate	right	11 males 9 females	Ao Tang Khen[3]	1990. Sep.
U. annulipes	lateral	random	10 males 6 females	Ao Nam Bor[1] Ao Tang Khen[3]	1990. Sep. 1991. Jan.

[1] 7°50′ N; 98°24′ E
[2] 13°28′ N; 100°55′ E
[3] 7°44′ N; 98°25′ E

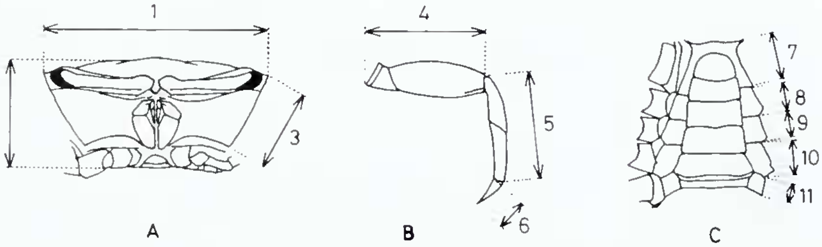

Figure 1. Diagrams of frontal view of carapace (A), ventral surface of left ambulatory leg (B), ventral view of male crab (C), and dimensions measured in this study. (1) carapace width: the minimum distance between both tips of the anterolateral angles. (2) body depth: the minimum distance between the carapace and a straight line in contact with the plane of the sterna with the first and second ambulatory legs. (3) carapace depth: the minimum distance between the tip of one anterolateral angle and the edge of the buccal region on the side of the Milne-Edwards opening. (4) I-section: the minimum distance between the inner edge of the basis and the outer edge of the merus of the thoracic legs. (5) II-section: the minimum distance between the inner edge of the carpus and the outer tip of the propodus of the thoracic legs. (6) III-section: the minimum distance between the inner edge and the tip of the dactylus of the ambulatory legs. (7), (8), (9), (10), and (11) the length of each sternum with cheliped, first, second, third and fourth ambulatory leg, respectively.

annulipes ($P < 0.001$), and in the I-section of the first ambulatory legs only of male *U. tetragonon* ($P < 0.01$). The asymmetry ratios of *U. annulipes* male crabs were 1.09 ± 0.01, 1.06 ± 0.02 and 1.05 ± 0.02, and the degree of asymmetry decreased posteriorly. The ratio for male *U. tetragonon* was 1.02 ± 0.01.

Total lengths of the minor cheliped and the first ambulatory leg on minor cheliped side tended to be greater in males than in females, and the difference was significant ($P < 0.05$) in *U. dussumieri*, *U. tetragonon* and *U. annulipes* for the minor chelipeds, and in *U. dussumieri* and *U. tetragonon* for the first ambulatory legs (Fig. 2). In addition, the same tendency ($P > 0.05$) was observed for the total length of the second ambulatory leg in the four species other than *U. annulipes*. The total length of the third ambulatory legs did not differ between male and female crabs. The total length of the fourth ambulatory leg was greater in female *U. tetragonon* than in male crabs ($P < 0.05$).

The body depths of male crabs were larger on the major cheliped side than on the other side ($P < 0.001$) (Table IV). The asymmetry ratios were between 1.05 and 1.07 for all species, indicating no difference between the species. The body depths of female crabs of all five species were symmetrical ($P < 0.05$).

The relative body depths on the major cheliped side of male crabs were larger than those of female crabs ($P < 0.05$). The relative body depth on the side bearing the minor cheliped in male crabs showed a similar tendency, especially in *U. dussumieri* and *U. tetragonon* ($P < 0.05$).

Table II

Carapace width and wet weight in Uca *spp.*

Species	Carapace width (mm)		Wet weight (g)	
	Male	Female	Male	Female
U. urvillei	25.19 ± 1.43 (23.40–26.75)	23.07 ± 1.49 (20.85–25.35)	5.030 ± 0.709 (4.115–6.169)	2.989 ± 0.604 (2.309–4.136)
U. dussumieri	29.80 ± 1.18 (27.65–32.85)	23.31 ± 1.03 (21.70–24.95)	9.273 ± 1.161 (7.371–12.553)	3.490 ± 0.508 (2.680–4.646)
U. vocans	23.05 ± 0.63 (22.15–24.55)	17.17 ± 0.66 (16.15–18.05)	5.503 ± 0.298 (4.865–5.930)	1.487 ± 0.294 (1.191–1.955)
U. tetragonon	21.00 ± 0.87 (19.40–23.35)	21.03 ± 0.93 (19.10–22.95)	3.754 ± 0.563 (2.956–5.465)	3.090 ± 0.339 (2.333–3.605)
U. annulipes	15.49 ± 0.79 (14.35–17.50)	11.98 ± 0.60 (10.95–12.50)	1.319 ± 0.229 (0.978–1.910)	0.437 ± 0.048 (0.355–0.495)

Mean ± the 95% confidence interval.
Numbers in parentheses indicate the range.

Table III

Weight of chelipeds relative to whole body wet-weight in Uca *spp.*

Species	Male crab		Female crab	
	Major side	Minor side	Right side	Left side
U. urvillei	0.366 ± 0.047 (31.48 ± 7.15)*	0.012 ± 0.001	0.016 ± 0.001 (1.02 ± 0.04)	0.016 ± 0.001
U. dussumieri	0.358 ± 0.015 (31.07 ± 2.12)*	0.012 ± 0.001	0.015 ± 0.001 (1.01 ± 0.07)	0.015 ± 0.001
U. vocans	0.432 ± 0.034 (40.18 ± 4.35)*	0.011 ± 0.000	0.015 ± 0.002 (0.98 ± 0.04)	0.016 ± 0.001
U. tetragonon	0.340 ± 0.013 (17.58 ± 1.13)*	0.019 ± 0.001	0.022 ± 0.001 (1.01 ± 0.02)	0.022 ± 0.001
U. annulipes	0.380 ± 0.032 (28.41 ± 4.41)*	0.014 ± 0.001	0.018 ± 0.001 (1.00 ± 0.00)	0.018 ± 0.001

* Student's *t*-test, $P < 0.001$.
Mean ± the 95% confidence interval.
Numbers in parentheses (mean ± the 95% confidence interval) indicate the asymmetry ratio based on weight (male crab = major cheliped side/minor cheliped side; female crab = right side/left side).

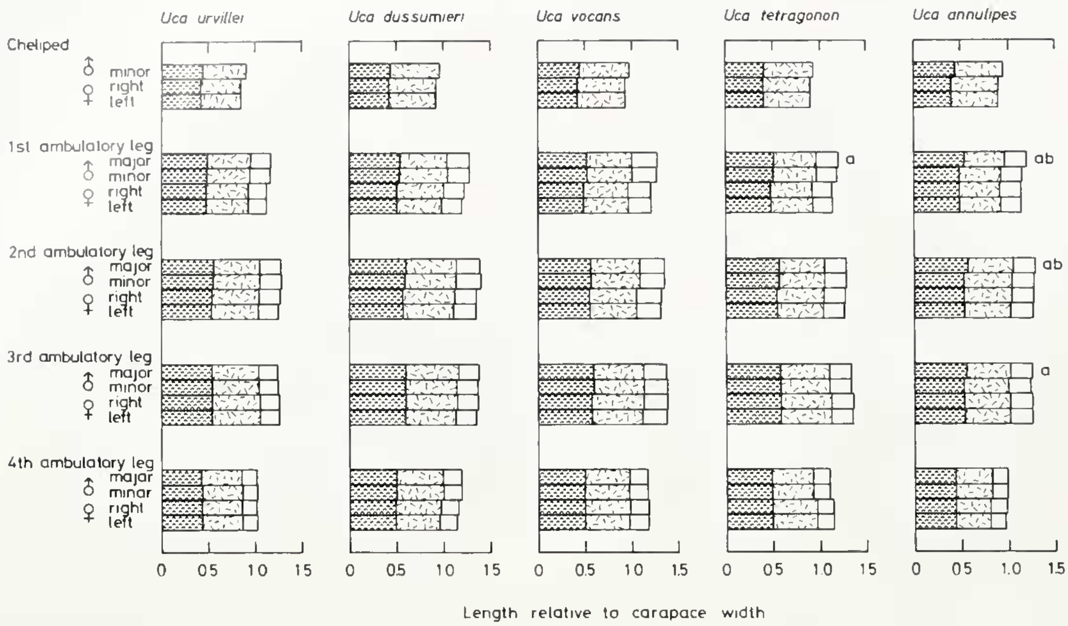

Figure 2. Length of the three sections of the thoracic leg relative to carapace width in *Uca* spp. Each bar shows the relative length of the I-, II- and III-section (Fig. 1B) from the left. (a), (b): asymmetry in the length of I-section of the thoracic leg and in the total length of the thoracic leg, respectively.

The carapace depths of crabs was symmetrical ($P < 0.05$) in both sexes of the four species other than in male *U. vocans* (Table V).

In the male crabs of all species, the sternum bearing the major cheliped was larger than that bearing the minor cheliped ($P < 0.001$), and the asymmetry ratios were between 1.16 and 1.19 (Fig. 3). The asymmetry is probably due to the hypertrophy of the coxa of the major cheliped, as indicated by the remarkable development of the propodus of the major cheliped (see Fig. 1C). In the male crabs of all species, the total length of the five sterna with thoracic legs was greater on the major cheliped side than it was on the opposite side, showing significant asymmetry ($P < 0.05$).

Male crabs of *U. urvillei*, *U. dussumieri* and *U. vocans* had larger major cheliped-bearing sterna than did female crabs of the same species ($P < 0.05$). But, there was no significant difference between male and female crabs of *U. tetragonon* and *U. annulipes* ($P > 0.05$).

The total length of the five sterna on the minor cheliped

Table IV

Length of body depth relative to carapace width in Uca *spp.*

Species	Male crab		Female crab	
	Major side	Minor side	Right side	Left side
U. urvillei	0.53 ± 0.01 (1.06 ± 0.01)*	0.50 ± 0.01	0.48 ± 0.01 (1.00 ± 0.01)	0.48 ± 0.01
U. dussumieri	0.58 ± 0.01 (1.07 ± 0.01)*	0.55 ± 0.01	0.52 ± 0.01 (1.00 ± 0.01)	0.52 ± 0.01
U. vocans	0.56 ± 0.01 (1.07 ± 0.01)*	0.53 ± 0.01	0.49 ± 0.02 (1.00 ± 0.01)	0.49 ± 0.03
U. tetragonon	0.56 ± 0.01 (1.05 ± 0.00)*	0.54 ± 0.01	0.51 ± 0.01 (1.00 ± 0.00)	0.51 ± 0.01
U. annulipes	0.55 ± 0.01 (1.05 ± 0.01)*	0.53 ± 0.01	0.52 ± 0.02 (1.00 ± 0.02)	0.52 ± 0.01

* Student's *t*-test, $P < 0.001$.
Mean ± the 95% confidence interval.
Numbers in parentheses (mean ± the 95% confidence interval) indicate the asymmetry ratio (male crab = major cheliped side/minor cheliped side; female crab = right side/left side).

Table V

Length of carapace depth relative to carapace width in Uca *spp.*

Species	Male crab		Female crab	
	Major side	Minor side	Right side	Left side
U. urvillei	0.34 ± 0.01 (1.02 ± 0.02)	0.34 ± 0.01	0.32 ± 0.01 (1.00 ± 0.01)	0.33 ± 0.01
U. dussumieri	0.33 ± 0.01 (1.01 ± 0.01)	0.33 ± 0.01	0.32 ± 0.01 (1.00 ± 0.01)	0.32 ± 0.01
U. vocans	0.31 ± 0.01 (0.98 ± 0.01)*	0.32 ± 0.01	0.31 ± 0.01 (0.99 ± 0.01)	0.31 ± 0.01
U. tetragonon	0.31 ± 0.00 (1.00 ± 0.01)	0.32 ± 0.00	0.30 ± 0.00 (1.00 ± 0.00)	0.31 ± 0.00
U. annulipes	0.33 ± 0.00 (1.00 ± 0.01)	0.33 ± 0.00	0.32 ± 0.01 (1.00 ± 0.01	0.32 ± 0.00

* Student's *t*-test, $P < 0.05$.
Mean ± the 95% confidence interval.
Numbers in parentheses (mean ± the 95% confidence interval) indicate the asymmetry ratio (male crab = major cheliped side/minor cheliped side; female crab = right side/left side).

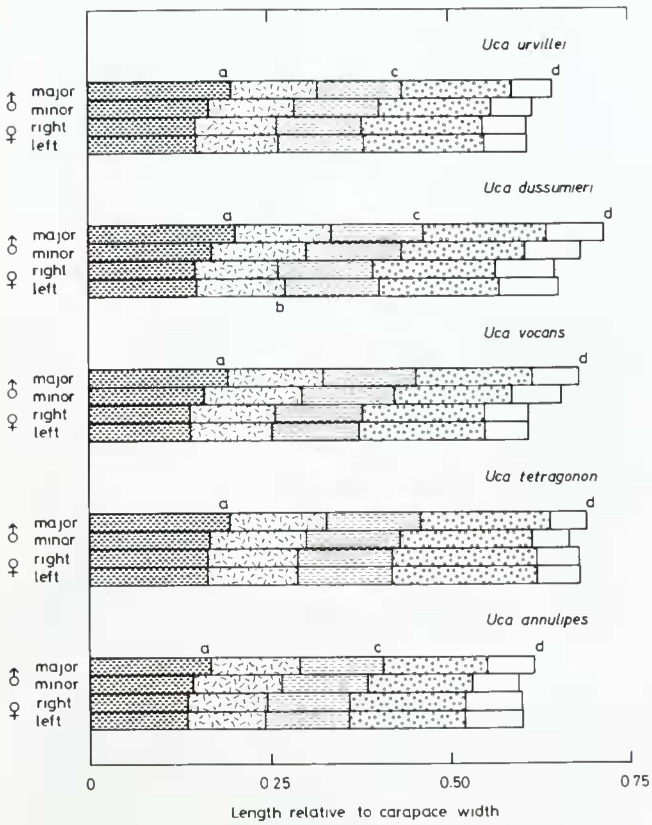

Figure 3. Length of each sternum bearing thoracic legs relative to carapace width in *Uca* spp. Each bar shows the relative length of the sternum bearing (from left to right) the cheliped, first, second, third and fourth ambulatory leg (Fig. 1C). (a), (b), (c), and (d) indicate asymmetry in the length of the sternum bearing the cheliped, first and second ambulatory leg, and in the total length of five sterna with thoracic legs, respectively.

side of male *U. dussumieri* and *U. vocans* tended to be larger than those of female crabs, and a similar, though weaker, tendency was observed in *U. urvillei*. The differences between the male and female crabs of *U. dussumieri* and *U. vocans* were caused by the male crabs having more extensive sterna bearing the cheliped and first ambulatory leg. The slight difference in the total length of the sterna of male and female *U. urvillei* was due to the smaller degree of enlargement of the sternum with the first ambulatory leg in male *U. urvillei*, compared with that of male *U. dussumieri* and *U. vocans*. On the other hand, female *U. tetragonon* and *U. annulipes* tended to have slightly longer sterna than the male crabs. This was because the sternum bearing the third ambulatory leg is remarkably larger in female crabs than in males, although the male crabs tended to have a larger sternum bearing the first ambulatory leg than did the female crabs.

Discussion

Male crabs of *U. annulipes*, which display with lateral waving, had longer first and second ambulatory legs on the major cheliped side than on the other side (Fig. 2), corresponding with the asymmetry reported for the lateral waver males of *U. pugilator* (Yerkes, 1901; Duncker, 1903; Huxley and Callow, 1933; Miller, 1973) and *U. pugnax* (Yerkes, 1901; Tazelaar, 1933). Moreover, comparing the major and minor cheliped sides, the I-sections of the first, second and third ambulatory legs were longer on the major cheliped side, resulting in asymmetry of total lengths of, especially, the first and second ambulatory legs. Male *U. tetragonon* have a form of display intermediate between the lateral and vertical waving types, and the I-section of their first ambulatory leg showed only asymmetry similar to that of the male *U. annulipes*. Asymmetry of the ambulatory legs was not seen in *U. urvillei*, *U. dussumieri* and *U. vocans* males, which display in the vertical form, or in females of any of the five species.

The sequence of the display performed by *U. annulipes* male crabs is as follows: the major cheliped, normally flexed in front of the buccal region, is extended laterally and subsequently raised, then flexed and brought down to the starting position from above the eyes and buccal region (Crane, 1957, 1975). The major cheliped constitutes about one-third of the whole body weight (Table III), and during such a display the proportion of its weight supported by each pair of ambulatory legs will change according to the angular position of the major cheliped. That is, while the flexed major cheliped is moving toward the side, its weight is borne on the anterior ambulatory legs and then on the ambulatory legs on the same side as the major cheliped. When the major cheliped is fully extended laterally, it achieves its maximum loading weight. Subsequently, during the raising of the unflexed major cheliped and its return to the starting position, the weight carried on the side of the body bearing the major cheliped will decrease gradually. The degree of asymmetry in the I-section of the ambulatory legs was greatest for the first ambulatory leg, and decreased gradually until no asymmetry was apparent for the fourth ambulatory legs (Fig. 2). Thus, the distances between the dactylus tips of each pair of ambulatory legs are greater anteriorly, especially on the side bearing the major cheliped, since waving males hold the I-section horizontally rather than vertically (Crane, 1975, Fig. 92). In addition, the distance between the dactylus tips of the first and fourth ambulatory legs is greater on the major cheliped side than on the other side, since the ambulatory legs of both sides were extended in the antero-posterior direction during display. The increased horizontal distance on the major cheliped side may be a morphological adaptation to bearing most of the weight of the major cheliped as it moves laterally from the anterior position during display.

On the other hand, in the sequence of the display of male *U. urvillei*, *U. dussumieri* and *U. vocans*, the major cheliped initially remains flexed in front of the buccal region, and is moved up and slightly forward, without unflexing (Crane, 1957, 1975). In such a display, the horizontal component of the motion of the major cheliped will be very small in both the antero-posterior direction and laterally, compared with the display of the lateral wavers. Therefore, the crab does not have to bear an additional load on the side of the major cheliped during waving. Vertical wavers, therefore, do not have an elongated I-section of the ambulatory legs on the major cheliped side.

The display performed by male *U. tetragonon* is intermediate between the lateral and vertical waving types (Crane, 1957, 1975). That is, the major cheliped, flexed in front of the buccal region, is incompletely extended forward at an acute angle. Subsequently, the semi-flexed cheliped is raised so that its tip barely reaches to the eye. In such a display, the crab does not have to bear a load on the ambulatory legs of the major cheliped side, as the lateral wavers do.

The asymmetry in the total length of the ambulatory legs or in the length of each section of the ambulatory leg was not seen in *U. vocans*, in which right-handed males are predominant (Takeda and Yamaguchi, 1973), or in male *U. urvillei* and *U. dussumieri* in which the ratio of left and right handedness is similar (Fig. 2). These facts suggest that the asymmetry of the ambulatory legs corresponds with differences in the form of display, rather than with differences in the mechanism inducing hypertrophy of one of the chelipeds, whether innate or random.

The ratio of body depth to carapace width was greater on the side bearing the major cheliped than it was on the opposite side, in male crabs of all species (Table IV). However, the relative carapace depth, which is considered to be related directly to the body depth, was the same on the two sides of the body (Table V). On the other hand, the length of the sternum bearing cheliped was much greater on the major cheliped side than it was on the minor cheliped side, resulting in the asymmetry of the body depth. Because the body depth was measured as the minimum distance between the carapace and a straight line in contact with the planes of the sterna bearing the first and second ambulatory legs (Fig. 1A), the excessive increase in the body depth on the major cheliped side, resulting from the excessive enlargement of the sternum bearing the major cheliped, means that the plane of the sternum with the major cheliped was inclined more vertically than was that of the opposing sternum. This more vertical sternum position probably contributes to the smoother motion of the major cheliped in a vertical direction.

The total length of the five sterna on the side with the minor cheliped in male *U. urvillei*, *U. dussumieri* and *U. vocans* tended to be greater than that of the female crabs (Fig. 3). But, there was no such sexual dimorphism in *U. tetragonon* and *U. annulipes*. These results indicate that the sterna on the minor cheliped side of males extend further laterally, like those on the major cheliped side, and that the plane of the sternum bearing the minor cheliped becomes more vertical than is the case in females of the vertically waving species.

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